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Quantified moorland vegetation and assessment of the role of burning over the past five millennia

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Abstract

Aims: To apply the Landscape Reconstruction Algorithm (LRA) to pollen count data from multiple sites to estimate local vegetation abundance and compare with charcoal-derived records of burning.

Location: Exmoor, southwest England, UK

Methods: Pollen count data from 16 sites were transformed to estimates of distance-weighted vegetation abundance using the LRA (REVEALS and LOVE models), correcting for bias in pollen production and dispersal. Charcoal concentration data from six sites were normalised using box-cox transformation to produce z-scores. Moving-window correlation was undertaken to compare pollen percentage values for key taxa (*Calluna*, Poaceae) and localised burning. Estimates of distance-vegetation abundance (LRA output) and time-averaged charcoal z-scores were compared to assess the role of burning as a driver for upland vegetation cover.

Results: Comparison of pollen percentage and normalised charcoal z-scores show little correlation between vegetation cover and burning. Estimates of distance-weighted vegetation abundance and normalised charcoal data show relationships between vegetation change and burning at four of the six sites. The relationships are site-specific: three sites suggest burning promoted grass-dominated vegetation, at one site burning promoted heather-dominated vegetation, and in two sites there is no apparent relationship.

Conclusions: The patterning of vegetation within uplands is a crucial part of ecosystem service delivery, and contemporary and future management benefits from understanding of 'long-term' development i.e. patterns over millennia. The correction of biases within pollen production and

dispersal to produce local vegetation estimates has demonstrated spatial heterogeneity in vegetation cover on Exmoor that is not otherwise evident in the pollen percentage data (which retains a strong influence of the regional vegetation cover). The relationship between LRA-derived vegetation cover and burning is not apparent in comparisons between pollen percentage data and charcoal records. This implies that studies that use pollen proportional data alone can misrepresent the relationship between vegetation cover and fire. This study demonstrates that fire has been an important part of the development of this cultural landscape.

Keywords

Pollen; charcoal; Exmoor; Landscape Reconstruction Algorithm; REVEALS; LOVE; Holocene; *Calluna*

Nomenclature

Stace (2010) for plants; Bennett (2007) for pollen taxa

Abbreviations

PPE: pollen productivity estimate; ***LRA***: Landscape Reconstruction Algorithm; ***REVEALS***: Regional vegetation estimates from large sites; ***LOVE***: Local vegetation estimates; ***subscript PP***: pollen percentage; ***subscript DWPA***: distance-weighted plant abundance; ***cal. yr BP: c***alibrated years before present (present = 1950)

Running head

Long-term upland moorland vegetation and burning

Introduction

Moorlands and uplands are highly valued landscapes as they deliver a wide range of ecosystem services including: water supply to lowlands; locations for agricultural production (in particular seasonal grazing); internationally-important sinks of greenhouse gases including carbon and methane; and are locations favoured for recreational activities (Reed et al. 2009). They are also areas that preserve and conserve nationally-important cultural heritage, including the traces of past society (Riley and Wilson-North 2001). A significant component of this ecosystem service delivery is the vegetation patterning of uplands, as many of the services are mediated through vegetation. Ecological research has focussed on understanding what controls upland vegetation, and points towards the importance of grazing, burning and climatic change (e.g. Yeo & Blackstock 2002). In the case of burning in particular, debates have become polarised and there is now a narrative of burning being predominantly damaging to upland moorlands (Davies et al. 2016). Datasets that look at differences through time, as well as space, can help to develop an appropriate evidence basis. Re-survey at known locations after 35-years on Scottish moorlands has been considered as a 'long-term' dataset (Britton et al. 2016) and these data offer excellent ecological observations. Although the temporal resolution of palaeo-ecological approaches cannot compare to ecological monitoring or measurement, they make it possible to observe change and infer processes that control this change over decadal to millennial timescales (Davies & Bunting 2010) and have the potential to identify vegetation responses over lag times longer than those afforded by ecological monitoring (e.g. Tinner et al. 1999).

A challenge to the application of palaeoecological datasets, and in particular pollen-based reconstructions, is bridging the gap between highly-detailed records of change over time from a small number of locations within a region and modern ecological survey data (e.g. many quadrats, or remote-sensed data). There are also significant differences in the ways that vegetation is recorded, and making pollen proportions from within a sedimentary basin commensurate with modern vegetation data (from field survey or remote-sensed datasets) poses major translational challenges. Various approaches to transformation of pollen into measures of land cover exist, although most are at best semi-quantitative and do not always produce strong matches between land cover and modern vegetation (Woodbridge et al. 2014). The relationship between pollen proportions and vegetation cover is non-linear (Sugita et al. 1999), confounded by differential pollen production and dispersal between taxa, and the nature of the regional (background) vegetation. Developments in understanding the pollen-vegetation relationship have resulted in improved approaches to the quantification of vegetation cover within the source area of pollen sites and resulted in the LRA

(Sugita 2007a, b). Much effort has gone into the parameterisation of this new approach (Broström et al. 2008; Mazier et al. 2012), and it is now possible to estimate the relative abundance of key taxa around pollen sites separate from the 'background' vegetation (e.g. Cui et al. 2013; Trondman et al. 2016). Where networks of pollen sites exist, it is possible to generate spatially-explicit, quantified past vegetation abundances using pollen count data.

This paper applies the LRA to pollen data from Exmoor, southwest England, to address a long-standing issue around a key driver of moorland vegetation, namely the importance of burning on vegetation character over the past 5000 years. Understanding local-scale vegetation patterning is important as 'standard' upland pollen sequences can include a significant background element making is difficult to differentiate the local from the background (Bunting et al. 2008). Previous work has indicated that Exmoor is a landscape with a long history of human land use spanning at least the last 5000 years. The earliest indicators of human occupation are remains of a hunter-gatherer camp site at Hawkcombe Head dating to around 7200 cal yrs BP; monuments dating to the later Neolithic and Bronze Age (c. 5000-3500 cal yrs BP) include stone settings, circles and funerary monuments (Riley & Wilson-North, 2001), and there are extensive remains of prehistoric field systems thought to date broadly from the middle Bronze Age (from 3500 cal yrs BP). Pollen stratigraphic studies have shown that the vegetation has been influenced by people throughout the past 5000 years (Fyfe et al. 2003; Fyfe 2012). Whilst traditional pollen percentage diagrams can indicate local-scale differences in vegetation (e.g. Davies & Tipping 2004), as stressed, these comparisons are confounded by pollen from the wider region. Application of the LRA will allow this background component to be removed, leaving a significantly clearer picture of local-scale vegetation around each pollen site (Sugita et al. 2010). Comparison with charcoal records (as a proxy for management using fire) will allow assessment of the role of burning in determining local vegetation character.

Materials and Methods

Estimates of local vegetation abundance were made using the LRA (Sugita 2007a, b). The LRA is a two-step model-based correction algorithm that can be applied to pollen count data to estimate vegetation abundance. The first step is to estimate regional vegetation abundance using the REVEALS model from pollen data that is thought to represent regional vegetation, such as large lakes (>50 ha sensu Sugita 2007a). The second step is to estimate local vegetation abundance using the

LOVE model applied to pollen counts from target sites, taking in to account regional vegetation cover (Sugita 2007b). The LRA requires pollen count data from chronologically-constrained sequences, pollen productivity estimates (PPEs) that are expressed relative to a reference taxon and estimates of the fall speed of the key pollen taxa for which estimates are required (Broström et al. 2008). PPEs have been measured across Europe by measuring modern pollen loading at networks of sites, and comparing this against the surrounding vegetation cover. The LRA has a series of important assumptions (Sugita et al. 2010), of which the key ones include: the main agent of pollen transport and deposition to the site is through above-canopy winds; differences in height of release of pollen between taxa do not matter; there is no inter-taxonomic preservation bias within the pollen count data; regional vegetation is stationary; and PPEs are invariant through time.

Exmoor is an upland made of shales, siltstones and slates, and contains almost 20,000 ha of open moorland, rising to 519 m above sea level. The upland has a maritime climate, with precipitation between 800 in the east and up to 2000 mm per annum on the highest ground, and a temperature range from 2 degrees in winter to 21 degrees in summer. Raw count data from 16 dated pollen sequences from Exmoor was used as input to the LRA, although not all sites cover the same time duration (Figure 1 and Table 1). In the absence of large lakes, Sugita et al (2010) and Trondman et al (2016) have demonstrated it is possible to use a network of smaller sites to calculate the regional vegetation abundance. Count data from each site were aggregated into 500-yr contiguous time windows to facilitate correlation and comparison between sites. The PPEs used were those established within the LANDCLIM project (Mazier et al 2012) and represent average PPEs from multiple empirical studies within Europe (SI Table 1). The LRA was run separately for each site. The data from the 'target' site in each run was used as input to the LOVE model, but excluded from the estimate of regional vegetation. Resulting values are a distance-weighted plant abundance (expressed as a percentage) within what is termed the necessary sources area of pollen *sensu* Sugita (2007b), i.e. the distance at which all abundance estimates for all taxa lie between 0-100 % (to within 1 standard error). The LOVE model produces local distance-weighted plant abundance for each taxon (expressed as a percentage of total cover). LOVE output is differentiated from original pollen percentage using the subscript DWPA (i.e. $Poaceae_{DWPA}$); pollen percentage results are described using the subscript PP (i.e. $Poaceae_{PP}$). Taxon-specific output of the REVEALS model are described using the subscript RV (i.e. $Poaceae_{RV}$)

Charcoal data is only available from six of the 16 sites. Charcoal counts exist in two size fractions: 10-50 µm and 50-180 µm. Charcoal counted from pollen slides is typically used to infer a regional fire signal (Mooney and Tinner 2011). Charcoal in larger size fractions in thin section preparations (>50 µm) is used to infer localised burning (Clark 1988). There is also support for the use of larger charcoal fractions from pollen preparations to infer localised burning (e.g. Pitkanen et al. 1999; Tinner et al. 2001). As a result, the coarse (50-180 µm) size fraction is used under the assumption that this reflects more localised burning. Whilst the source area cannot be precisely determined, it is expected to be closer to the source area of pollen than the smaller charcoal size fraction. The data is expressed as concentrations of charcoal fragments cm^{-3} in the original publications. Charcoal records are standardised using z-scores (using the mean and standard deviation over the record) following a Box-Cox power transformation as described by Power et al (2010). Analysis of the charcoal data was undertaken using the palaeofire R-package (Blarquez et al. 2014). Average z-scores for each 500-yr time window have been calculated for comparison with *Calluna*$_{DWPA}$ and Poaceae$_{DWPA}$.

Comparison of the original pollen proportion data for select taxa (Poaceae$_{PP}$, *Calluna*$_{PP}$) and charcoal z-scores for the coarser charcoal fraction (50-180 µm) was undertaken by using a 10-sample moving-window Pearson's product moment correlation coefficient. Use of a moving window allows changes in the strength of relationships through time to be recognised (cf. Fyfe and Woodbridge 2012).

Results

Regional and local vegetation cover estimates

The results of the estimates of regional vegetation cover are shown for each time window in Figure 2 and describe the general development of the upland landscape. In the oldest time window, at 5500-6000 cal BP, regional woodland cover is estimated at around 60%, with half of this represented by *Corylus*$_{RV}$, followed by *Quercus*$_{RV}$ and *Ulmus*$_{RV}$. Open-ground taxa at this time are a mix of *Calluna*$_{RV}$ and Poaceae$_{RV}$. Woodland cover declines over successive time windows and is halved by 4000-4500 cal BP (to 30 % regional vegetation cover). Poaceae$_{RV}$ becomes the dominant regional vegetation cover at 5000-5500 cal BP, and generally increases. *Plantago lanceolata*$_{RV}$, which shows a continual presence from 5000 cal BP implies some improved grassland. *Calluna*$_{RV}$ varies around an average of 20 % cover from 3500 cal BP onwards.

The general regional patterns that emerges from the results of the REVEALS model hides considerable spatial variation that is shown when the LOVE model is applied to each pollen record (Figure 3). For clarity, only the *Calluna*$_{DWPA}$, Poaceae$_{DWPA}$ and *Plantago lanceolata*$_{DWPA}$ results are shown in detail, with 'other' largely representing woodland taxa. At 4000-4500 cal BP, when regional vegetation cover is around 60 % Poaceae$_{RV}$, some sites are almost entirely surrounded by Poaceae$_{DWPA}$ within the local vegetation (e.g. Long Breach at 95 % Poaceae cover) whilst others, even in close proximity, have a more mixed local vegetation (e.g. Gourte Mires, adjacent to Long Breach, has 48 % Poaceae$_{DWPA}$ and 35 % *Calluna*$_{DWPA}$). Other sites are pre-dominately *Calluna*$_{DWPA}$ (e.g. Spooners with 64 %). This local-scale vegetation patterning continues through all time windows, with sites close together supporting different local vegetation cover: in no time window is there a 'homogenous' signature. A second feature that is apparent both on Figure 3 and in examination of individual site transformations (see Supplementary Information Figures 1-6) is the scale of change of local vegetation between different time windows. The local vegetation estimates can show major differences between adjacent time intervals, indicating major changes in the character of vegetation at the temporal resolution of this study. .

Charcoal and pollen percentage/vegetation cover relationships

Comparison of z-scores for the 50-180 µm charcoal data and the original (non-aggregated) pollen percentage data from the six sites with charcoal data has been undertaken using moving-window correlation analysis to identify time-specific relationships between the dominant open ground taxa (Poaceae$_{PP}$ and *Calluna*$_{PP}$) and burning (Figure 4). Significant relationships between patterns of micro-charcoal and the pollen percentage data are uncommon and show no temporal or spatial relationship across sites. At Long Breach there is a strong positive relationship between charcoal and Poaceae$_{PP}$ between 6000-4500 cal BP, and again a significant relationship (at the 0.1 level) between 1500-1000 cal BP. Beckham and North Twitchen Springs has short-lived positive relationships around 3000-3500 cal BP between Poaceae$_{PP}$ and micro-charcoal z-scores. Beckham also shows a significant positive relationship between *Calluna*$_{PP}$ percentages and micro-charcoal z-scores between 3500-2500 cal BP. Only two other sequences indicate a relationship between *Calluna*$_{PP}$ and micro-charcoal, both negative correlations, at 4000-3500 cal BP for Gourte Mires and 1250-1000 cal BP for Long Breach.

Comparison of the z-scores for the 50-180 µm charcoal data at 500-yr time interval for *Calluna*$_{DWPA}$ and Poaceae$_{DWPA}$ are shown on Figure 5. Two sites show no apparent relationship between *Calluna*$_{DWPA}$ or Poaceae$_{DWPA}$ (Larkbarrow and North Twitchen Springs). Two sites show a clear positive relationship between Poaceae$_{DWPA}$ and charcoal z-scores through all time windows (Long Breach and Beckham). Higher charcoal z-scores in these sites are strongly associated with higher Poaceae$_{DWPA}$. A similar, but weaker, relationship can be observed at Gourte Mires. Relationships between *Calluna*$_{DWPA}$ and charcoal z-scores are absent from all sites with the exception of Swap Hill, where this is an apparent relationship from 5000-1500 cal BP: higher z-scores are associated with higher *Calluna*$_{DWPA}$, although the relationship does not appear to persist to the more recent time windows.

Discussions

Spatial heterogeneity in past upland vegetation and land cover

The LRA is a major advance on examination of pollen percentages, as it explicitly attempts to disentangle the regional pollen loading from the local vegetation signal (Sugita 2007a, b). Trondman et al. (2016) identified issues with dealing with potential 'on-site' vegetation including *Calluna* and Cyperaceae on bogs in southern Sweden. The Exmoor study has removed Cyperaceae from the pollen records in recognition of the likely strong local signal; however, *Calluna* is widespread across the upland in the present and not restricted to the small bogs that have been used here. It has thus been included as an important component of the vegetation of the upland. Whilst pollen-analytical methods do not allow the separation of grasses and it is assumed that the pollen originates from the main acid grassland species *Molinia caerulea*, *Agrostis stolonifera*, *Agrostis canina*, *Festuca* spp. and *Nardus stricta* (cf. Stevenson & Thompson, 1993; Stephenson & Rhodes, 2000). The size of the bogs used on Exmoor is very small (Table 1) and thus even local pollen is likely recruited from well beyond the extent of the bog.

The regional vegetation pattern for Exmoor shows a largely open landscape since 5500 cal BP, and the archaeological record of the upland that demonstrates significant human presence from at least 3500 cal BP (Riley & Wilson-North 2001). The LOVE-based vegetation estimates demonstrate strong differences between sites within the landscape that is not evident either from the REVEALS output or from the original pollen percentage data. Many studies have demonstrated patterning and

differences using pollen percentage data (e.g. Davis et al. 1980; Fyfe et al. 2003; Davies & Tipping 2004; Fyfe & Woodbridge 2012). Application of the LRA separates the local and regional pollen signals that exist in all pollen sequences, and this represents a major advance within pollen analysis. Local estimates of vegetation abundance for individual sites demonstrates periods of time when particular plants are not found in the local vegetation around the site, in spite of the significant presence in the pollen percentage diagram (SI figures 1-6). This has been recognised elsewhere, for example Cui et al. (2013) in southern Sweden have been able to successfully remove the impact of large pollen producers such as *Pinus* that otherwise confound local vegetation reconstruction. Mehl & Hjelle (2016) were also able to recognise plants that were common within the wider region but not within the local vegetation of their sites in western Norway (particularly *Betula* and *Pinus*).

Burning as a driver of moorland vegetation cover

Differences in the character of modern upland vegetation are normally explained through a combination of climatic gradients and land use. At the macro-scale (e.g. national scale) gradients in climate (oceanicity, temperature and rainfall) are strong determinants on moorland vegetation (Yeo & Blackstock 2002); however, within an upland block such as Exmoor these climatic gradients are marginal and are unlikely to be major determinants on vegetation composition. At the regional (e.g. Exmoor) scale, anthropogenic controls are a significant determinant on modern moorland vegetation, in particular burning frequency, grazing intensity and pollution (sulphur and nitrogen deposition) (Stephenson & Rhodes 2000; Yeo & Blackstock 2002). Over millennial time scales pollution can be discounted as this is elevated only in the post-industrial period. At the spatial scale of this study, drawing on sites within the same region and on the same upland, long-term climatic change may also be ruled out as an important control under the assumption that all sites will experience the same climatic shifts. Shifts in regional climate to wetter conditions might have an impact on raised bog vegetation (e.g. at 2800 cal BP: Pancost et al. 2004); the impact this may have on moorland vegetation is unclear when vegetation composition is not tightly coupled to bog surface wetness. Within the analysis presented here the temporal resolution (500 years) is insufficient to identify the impact of decadal or centennial-scale climate shifts. More temporally-detailed work would be necessary to identify such relationships, but there is currently no coherence between the vegetation estimates to suggest climate as an important regional driver.

The transformation of charcoal count data to normalised z-scores here allows direct consideration of the role of burning as an important driver of local moorland vegetation. Exploration of the

283 relationships between pollen percentages of key taxa and charcoal z-scores has shown few clear
284 relationships between burning and vegetation using moving window correlation (Figure 4). This is
285 similar to the findings of Fyfe & Woodbridge (2012), who also found few consistent relationships
286 between pollen proportions of key moorland taxa and fire, leading them to argue that fire alone was
287 not an important determinant of moorland vegetation. However, the results from application of the
288 LRA to the data from Exmoor show clear differences between pollen proportions and distance-
289 weighted vegetation abundances. When the LRA results are compared with the normalised charcoal
290 z-scores associations exist between grassland cover and burning at some sites throughout the
291 duration of the records (e.g. Long Breach and Beckham) and there is a weak relationship at Gourte
292 Mires. Modern ecological studies suggest that frequent or intense burning would promote grass-
293 dominance on moors, and this is frequently carried out as a management strategy to increase the
294 palatability of moorland vegetation for grazing animals (Hobbs & Gimingham 1987). Application of
295 the LRA allows this relationship to be extracted by considering only the local vegetation separate
296 from the regional background pollen rain. Palaeoecological studies by Chambers et al. (1999) and
297 Chambers et al. (2007), drawing on high-resolution (percentage-based) datasets have also noted
298 correlation between charcoal and increased Poaceae percentages over the past 500 years,
299 suggestive of more frequent or severe fires (Chambers et al. 1999). In this study, the results from
300 Swap Hill indicate a very different relationship between burning and local vegetation, with charcoal
301 z-scores correlating with *Calluna*$_{DWPA}$ cover, at least between 6000 and 1500 cal BP. Modern studies
302 demonstrate that low intensity rotational burning on a regular basis can promote heather
303 regeneration (Yeo & Blackstock 2002), although Davies et al. (2010) found through controlled
304 experimental burning regimes that the severity and frequency of the burning was less important
305 than the age structure of the *Calluna*: older stands have reduced capacity for vegetative
306 regeneration, and thus are reduced in extent. This points towards differentiated exploitation and
307 use of particular areas in relatively close proximity from prehistoric times on (Swap Hill and Beckham
308 are less than 1 km apart: Figure 1). At Swap Hill the weakening of the relationship between
309 *Calluna*$_{DWPA}$ and charcoal z-scores after 1500 cal BP suggests changes in land management practices
310 that ultimately break the link between burning and *Calluna* cover.

311

312 Two of the sites used in this study show no relationship between charcoal z-scores and either
313 Poaceae$_{DWPA}$ or *Calluna*$_{DWPA}$ (North Twitchen Springs and Larkbarrow). Chambers et al. (2007) also
314 recognise sites in south Wales that do not have this relationship (based on pollen percentage values
315 and macrofossil records), whilst others do. Other drivers of vegetation may thus have been
316 important, and Chambers et al. (2007) suggest that changes in grazing regimes (in particular changes

from cattle to sheep) could have been an important factor, although the evidence to support this is limited. Archaeological evidence for grazing (field systems, enclosures) extends back to at least 4,000 years BP on Exmoor (Riley and Wilson-North, 2001), and grazing intensity is likely to have varied both spatially and temporally. Coprophilious fungi can be used as indicators of grazing (Cugny et al. 2010), and Davies (2016) has utilised this approach in the Pennines (UK) to assess the role of grazing animals in recent moorland vegetation dynamics, finding associations between coprophilous fungi, contraction of heather and increases in Poaceae (pollen percentage-based) over recent centuries. The application of dung fungal spores on Exmoor is an avenue of research with high potential for further elucidating moorland vegetation - grazer interactions, and high-resolution coprophilous dung fungal records are in progress (Ombashi unpubl.). The relationship between burning, grazing and vegetation is rarely clear, and in the current absence of indicators for grazing such as coprophilous fungi, caution must be taken in attributing any one causal mechanism (including burning), as even with high-resolution datasets, multiple causal factors may result in similar palaeoecological signals (Chambers et al. 2007).

The main limitations on the application of the LRA in developing useful datasets to understand local-scale patterns of vegetation change, and the drivers of those changes, are two-fold. First, there are currently only a limited number of pollen taxa for which the key parameters (PPEs and fall speed) are available. The application of networks of small bogs has overcome the need to use large lakes from which regional vegetation estimates can be derived (this study; Sugita et al. 2010; Trondman et al. 2016), provided there are enough small bog records that can be used. Second, the necessity of correlation between sequences limits the temporal resolution that can be achieved, as all sites need to be reduced to time-equivalent samples. Within this study the limitations of the original age-depth models (age uncertainty of each sample) and the temporal sampling resolution (years between adjacent samples) necessitated a 500-yr time window. Moorland vegetation changes can occur on considerably shorter time-scales, for example Davies (2016) details regime shifts from *Calluna*-dominance to Poaceae dominance in the Pennines (UK) over periods of time as short as 25-85 years. Where higher-resolution sampling and age-depth models supported by more radiocarbon dates or other time-markers are available it may be possible to apply the LRA to shorter time windows (e.g. Fredh et al. 2016). The LRA-based approach does not replace the highly detailed, high-temporal resolution work from individual sites such as that of Chambers et al. (2007) and Davies (2016). This is essential in exploring burning/vegetation relationships, and future and ongoing research on Exmoor and other uplands which couples high-resolution pollen analyses with proxies for grazing such as coprophilous fungi will provide powerful, conservation-management oriented insights.

What these studies cannot do is disentangle and quantify local vegetation cover from the regional signal within the pollen datasets, although macrofossil analysis may go some way to qualitative interpretation of the records.

Conclusions

The analytical approach to transformation of pollen count data into local vegetation abundance has provided improved insights into the spatial patterning of vegetation. Within this particular region, clear differences within the nature of the local vegetation have been identified, in particular the relative importance of *Calluna* and Poaceae in moorland vegetation, that are not apparent from pollen percentage data alone. Differences between sites within the region, which all have the same geology and experience the same climate, are most likely to relate to human land use and management approaches over the past 5000 years. Burning and/or changes in grazing intensity are well-established controls on moorland vegetation in regions such as this. In the absence of data on past grazing regimes, burning regimes have been explored through examination of micro-charcoal records from six selected sites. At three sites, burning appears to promote and sustain grass-dominated vegetation, at one site it promotes and sustains heather-dominated vegetation (at least between 5500-1500 cal BP), and there is no clear signal from two others. Future research should focus on testing the role of grazing as a driver of vegetation cover and change using appropriate proxies for grazing such as coprophilous fungi.

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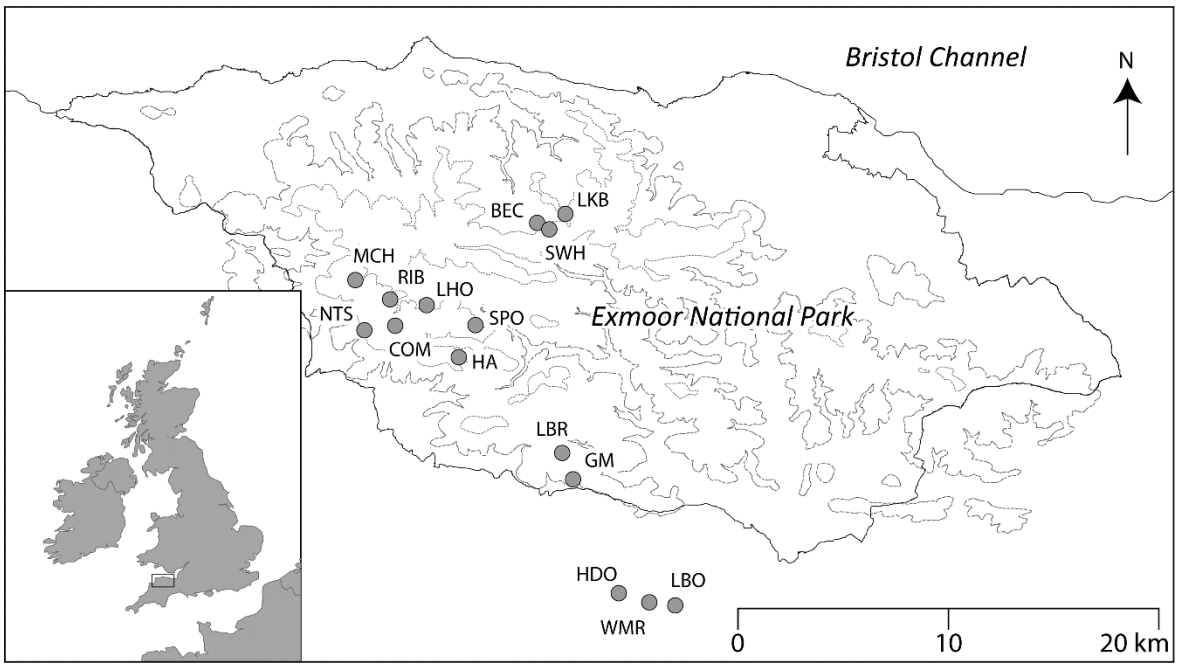
494 Figure 1: Location of sites used for LRA analysis on Exmoor. Dashed lines on panels indicate 50 m

495 contour lines; roads and main drainage lines are given. Details of sites and site codes are given on

496 Table 1.



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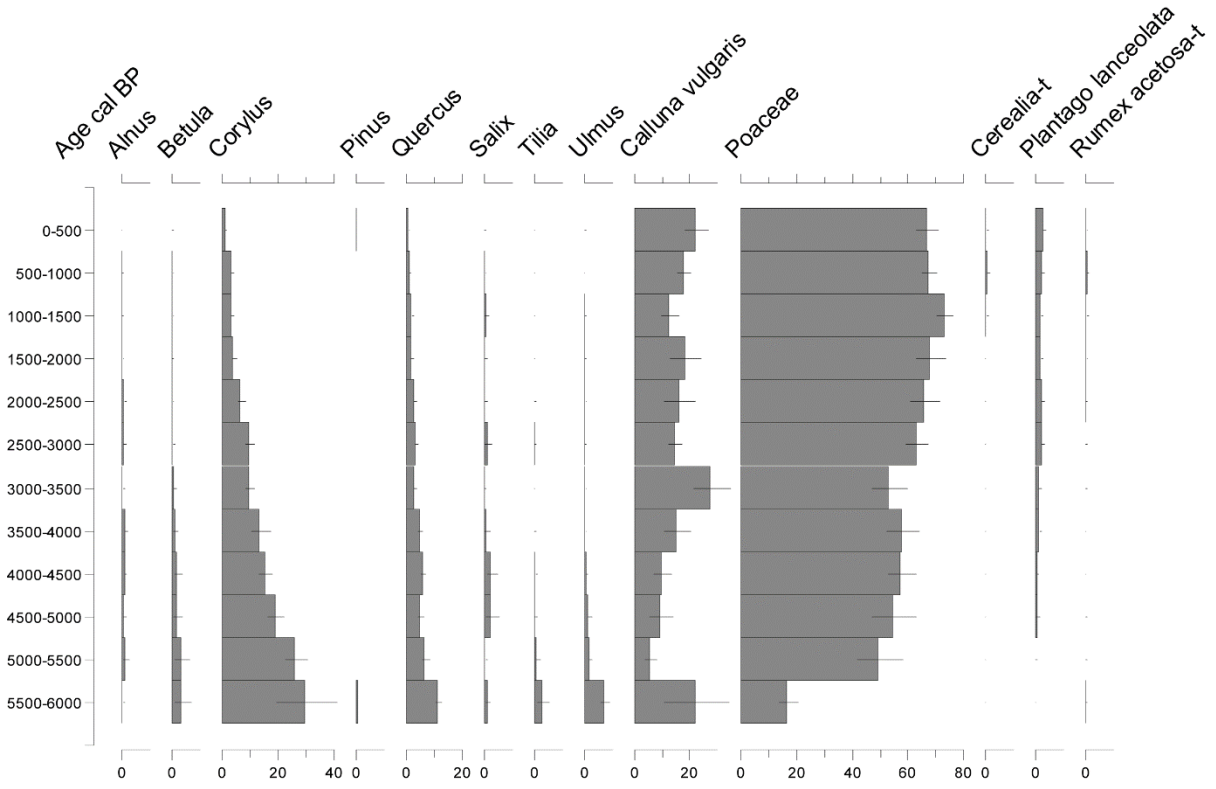
499 Figure 2: REVEALS-based regional vegetation estimates for Exmoor for main taxa based on 16 pollen

500 sequences.



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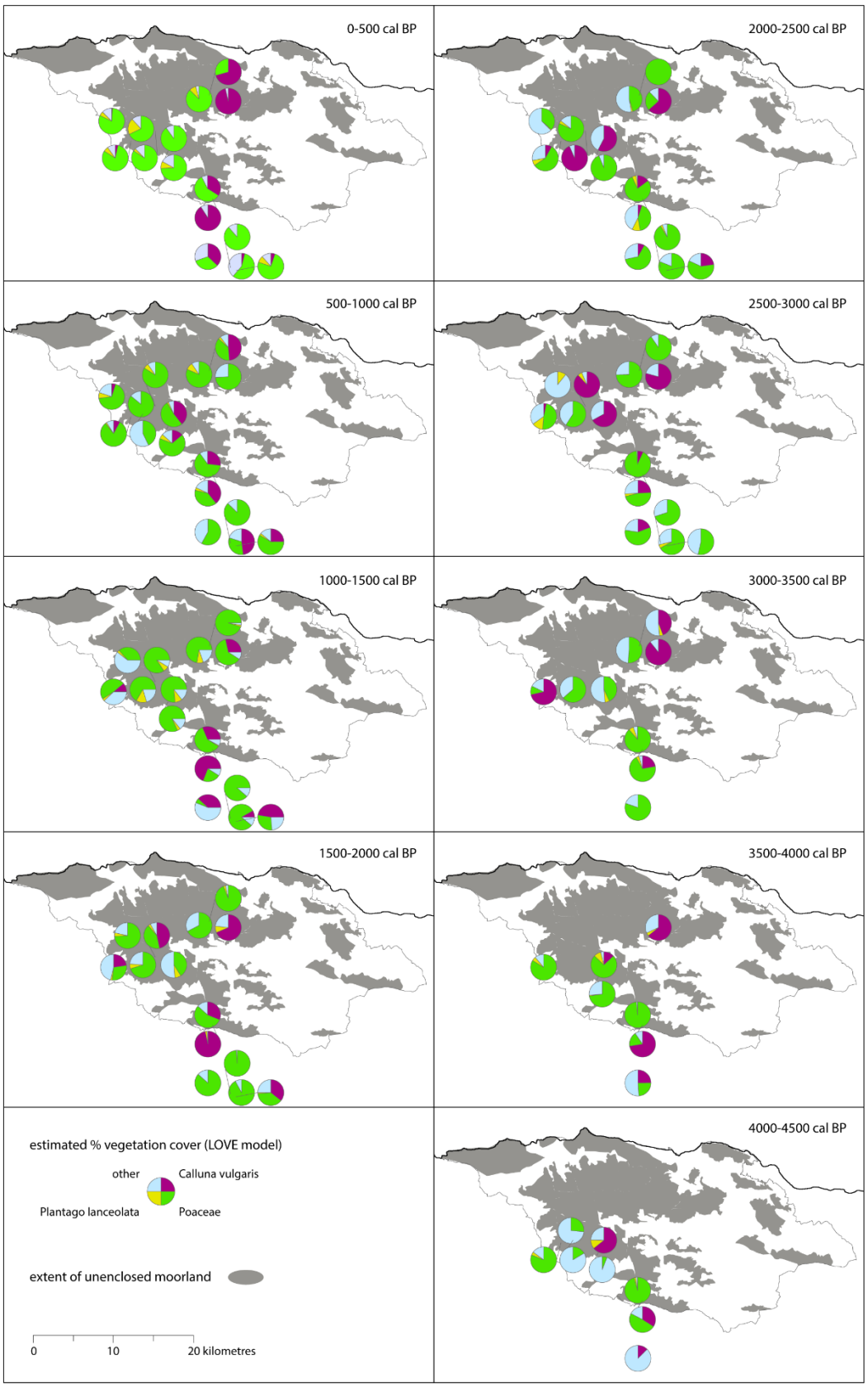
503 Figure 3: LOVE estimates of percentage distance-weighed cover of key moorland taxa for all sites on

504 Exmoor.



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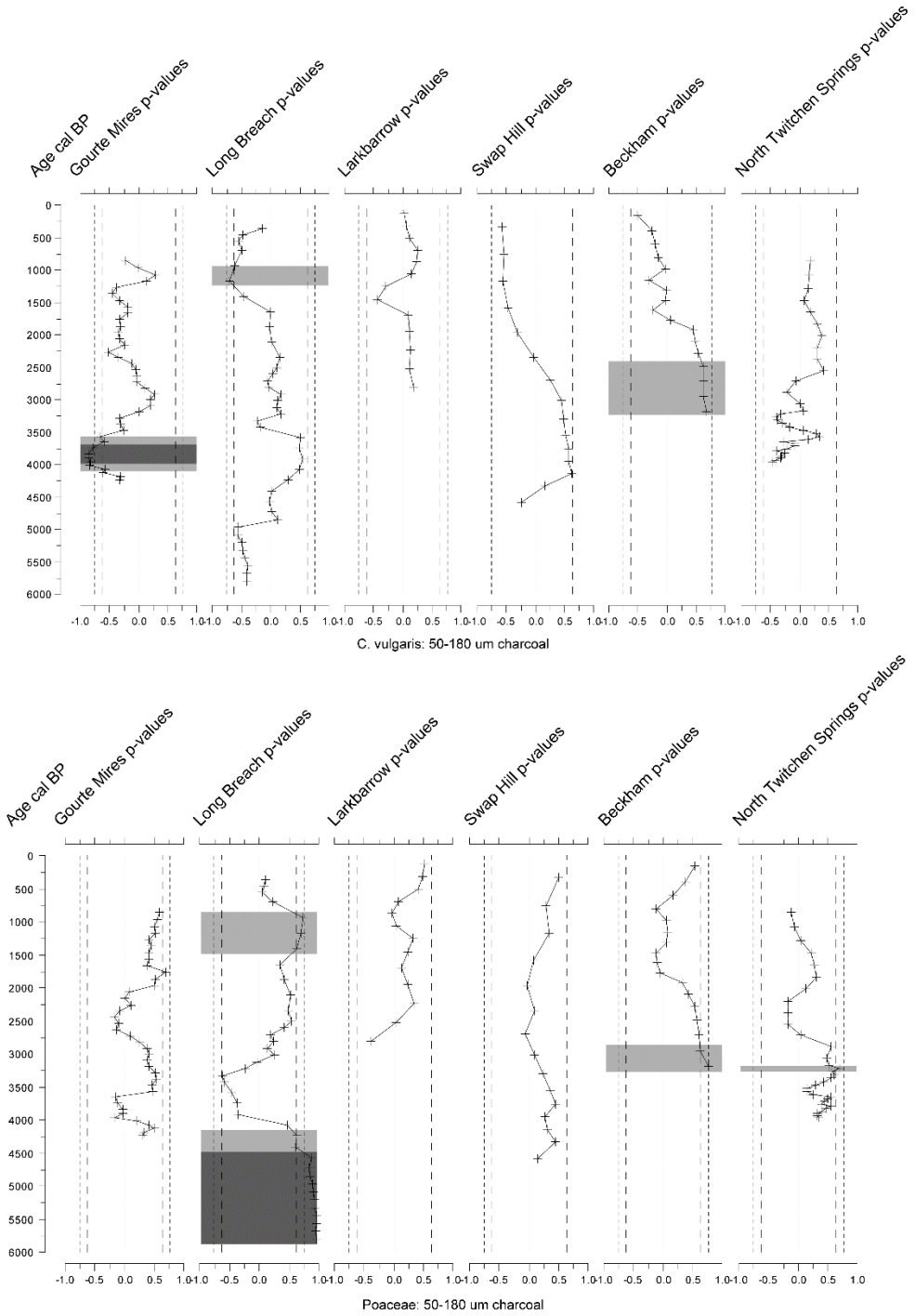
506 Figure 4: Pearson's product moment correlation coefficient scores for 10-sample moving window
507 between pollen percentage data (top: *Calluna*, bottom: Poaceae) and charcoal z-scores (50-180 µm
508 fraction). Long vertical dashed lines indicate significance level at p<0.1. Short dashed vertical lines
509 indicate significance level at p<0.01. Grey boxes indicate periods of significant relationships at the
510 0.1 and 0.01 level.



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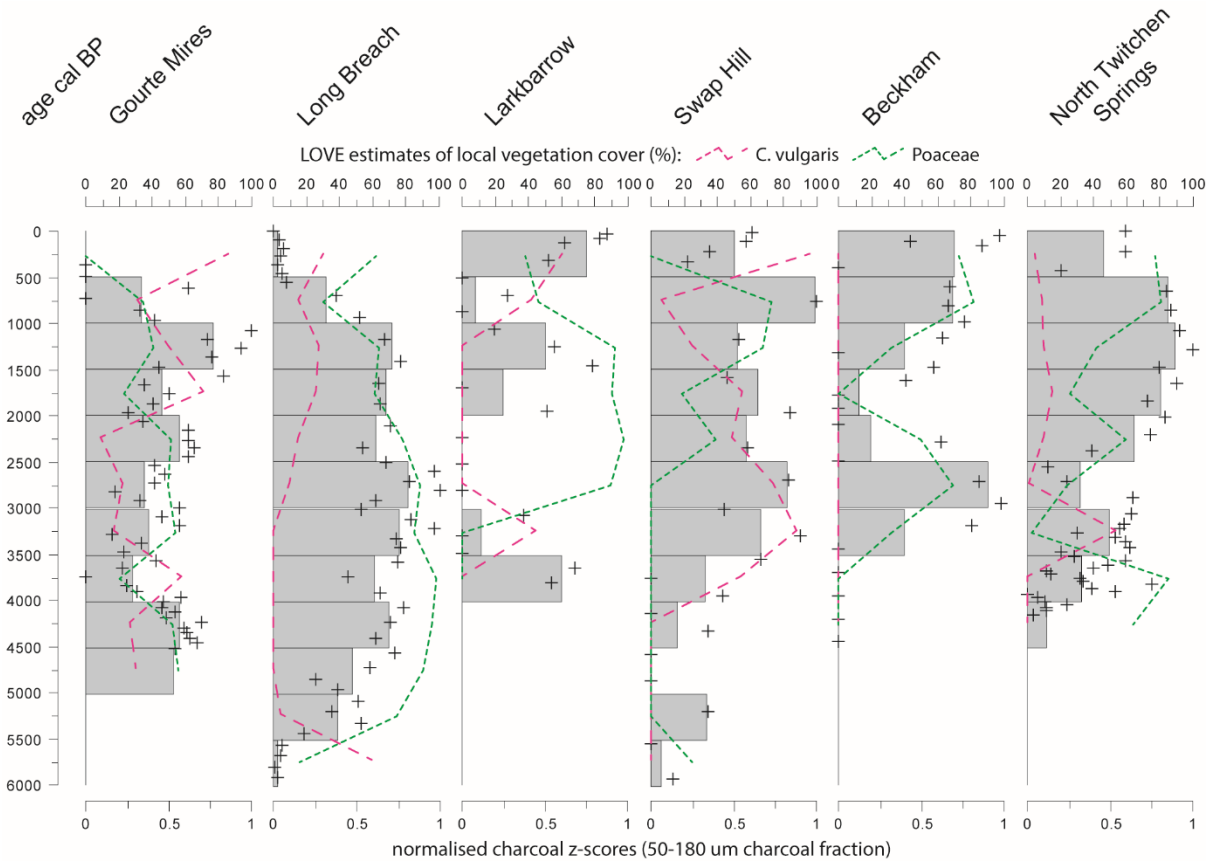
512 Figure 5: comparison between LRA estimates of distance weighted cover of *Calluna* and Poaceae,

513 and charcoal z-scores (50-180 µm fraction). + indicate charcoal z-scores; grey bars represent average

514 charcoal z-scores for each 500-yr time window for comparison with LOVE estimates.



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516 Table 1: Details of sites used for LRA on Exmoor. Sites marked with * include charcoal data. Codes
517 are those used on Figure 1. Locations are given as decimal degrees (WGS1984)
518

Site name (code)	Location	Elevation (m)	Site radius (m)	n 14C dates	Age range (cal BP)	Reference
Gourte Mires (GM)*	51.054, -3.678	291	20	4	4500-400	Fyfe et al (2003)
Long Breach (LBR)*	51.066, -3.687	339	30	5	6500-present	Fyfe et al (2003)
Long Holcombe (LHO)	51.107, -3.759	410	10	3	5300-present	Fyfe (unpublished)
Moles Chamber (MCH)	51.139, -3.833	421	15	6	3000-present	Fyfe (2012)
North Twitchen Spring (NTS)*	51.117, -3.826	352	15	5	4200-present	Fyfe (2012)
Roman Lode (RLO)	51.129, -3.783	442	50	2	2600-present	Fyfe (unpublished)
Comerslade (COM)	51.120, -3.805	447	100	6	8400-800	Fyfe (2012)
Larkbarrow (LKB)*	51.171, -3.688	378	50	4	3800-present	Davies et al (2015)
Swap Hill (SWH)*	51.164, -3.699	418	150	4	6400-present	Davies et al (2015)
Beckham (BEC)*	51.166, -3.706	392	30	4	4500-present	Davies et al (2015)
Ricksy Ball (RIB)	51.131, -3.809	430	10	8	6500-present	Fyfe (unpublished)
Spooners (SPO)	51.121, -3.750	412	60	3	8300-present	Fyfe (unpublished)
Windmill Rough (WMR)	50.975, -3.633	259	10	3	2600-present	Fyfe et al (2004)
Lobbs Bogg (LBO)	50.970, -3.624	242	15	5	2500-present	Fyfe et al (2004)
Hares Down (HDO)	50.978, -3.644	254	5	4	2600-present	Fyfe et al (2004)
Halscombe Allotment (HA)	50.989, -3.684	350	10	5	8800-200	Fyfe (unpublished)

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Supporting information to the paper

Fyfe, R.M., Ombashi, H., Davies, H. & Head, K. Moorland vegetation and burning over the past five millennia. *Journal of Vegetation Science*.

Appendix S1. Pollen productivity estimates and fall-speed of pollen used within the Landscape Reconstruction Algorithm

Table 1: Pollen productivity estimates, standard errors and fall speeds of pollen used as input parameters for the LRA. PPEs and SEs are taken from Mazier et al. (2012)

Taxon	PPE	Standard error	Fall speed (ms^{-1})
Abies	6.88	2.084	0.12
Alnus	9.07	0.011	0.021
Artemisia	3.48	0.039	0.025
Betula	3.09	0.072	0.024
Calluna vulgaris	0.82	0.001	0.038
Carpinus	3.55	0.181	0.042
Cerealia-t	1.85	0.146	0.06
Corylus	1.99	0.038	0.025
Fagus	2.35	0.012	0.057
Filipendula	2.81	0.185	0.006
Fraxinus	1.03	0.011	0.022
Poaceae	1	0.000	0.035
Juniperus	2.07	0.001	0.016
Picea	2.62	0.015	0.056
Pinus	6.38	0.200	0.031
Plantago lanceolata	1.04	0.009	0.029
Plantago media	1.27	0.033	0.024
Plantago montana	0.74	0.017	0.03
Quercus	5.83	0.023	0.035
Rumex acetosa-t	2.14	0.077	0.018
Salix	1.22	0.012	0.022
Secale-t	3.02	0.003	0.06
Tilia	0.8	0.001	0.032
Ulmus	1.27	0.003	0.032

Appendix S2. Pollen and distance-weighted vegetation estimates for individual sites with charcoal records from Exmoor.

Figure S2-1: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Swap Hill, Exmoor (original data from Davies et al. 2015).

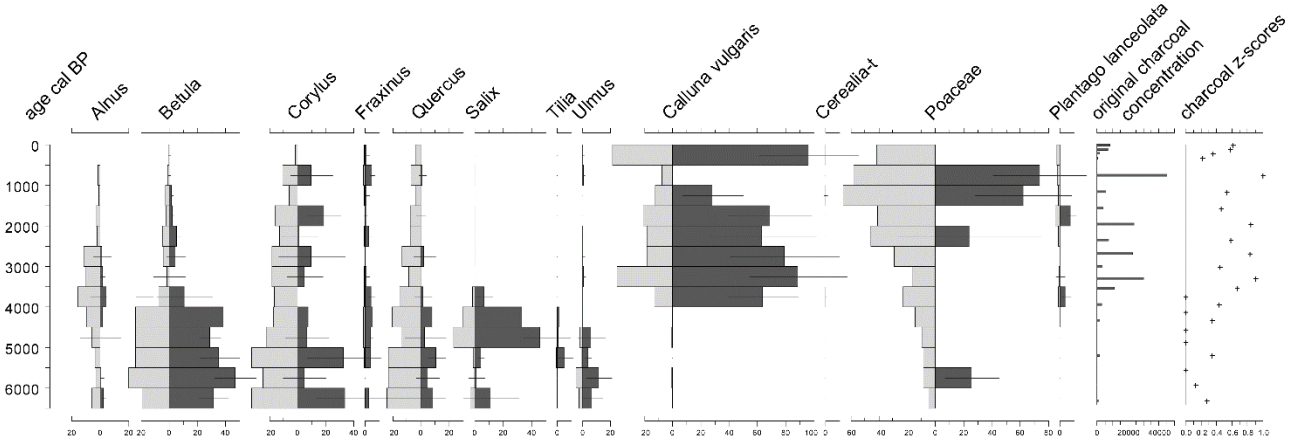


Figure S2-2: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Beckham, Exmoor (original data from Davies et al. 2015).

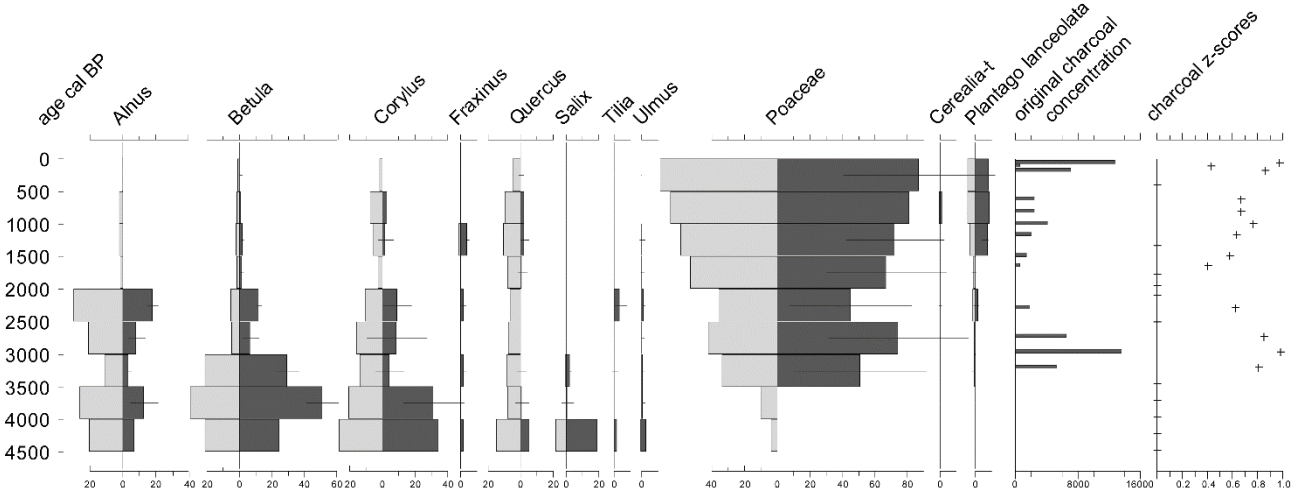


Figure S2-3: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Larkbarrow, Exmoor (original data from Davies et al. 2015).

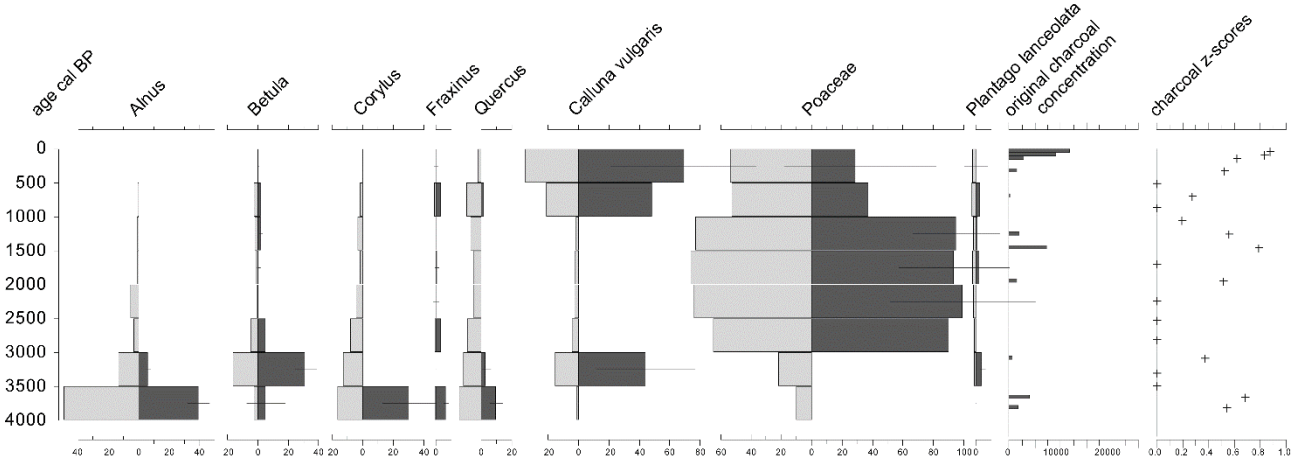


Figure S2-4: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Long Breach, Exmoor (original data from Fyfe et al. 2003).

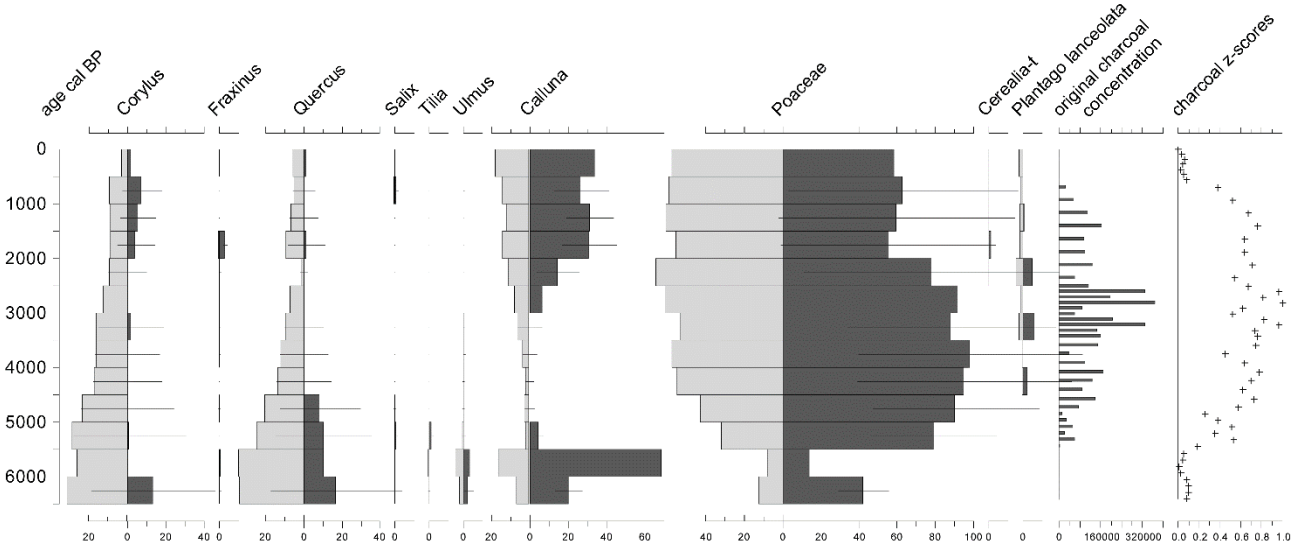


Figure S2-5: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Gourte Mires, Exmoor (original data from Fyfe et al. 2003).

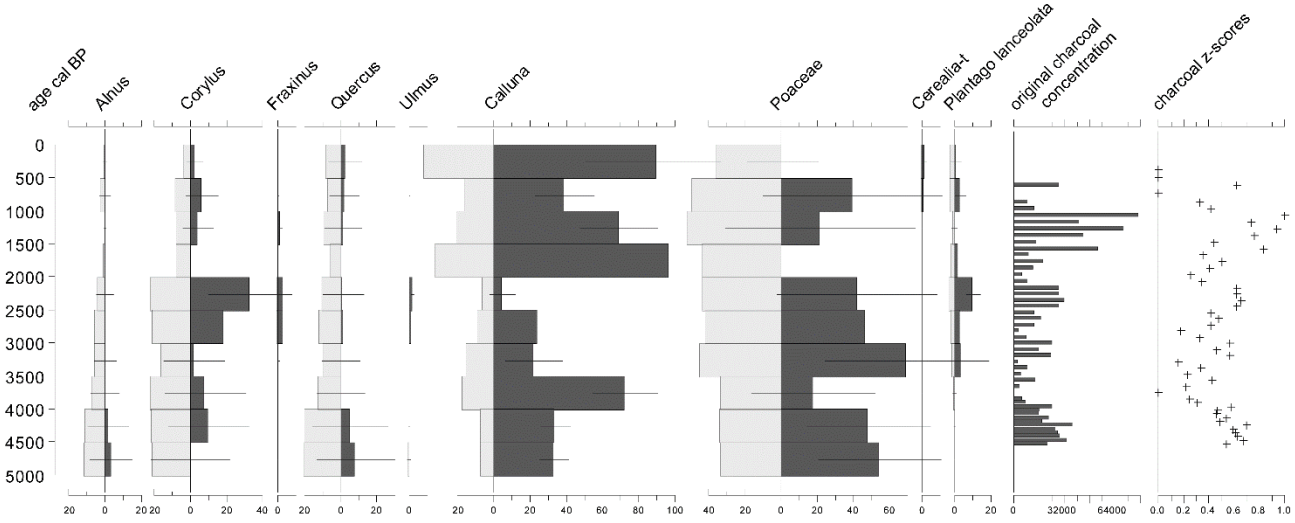
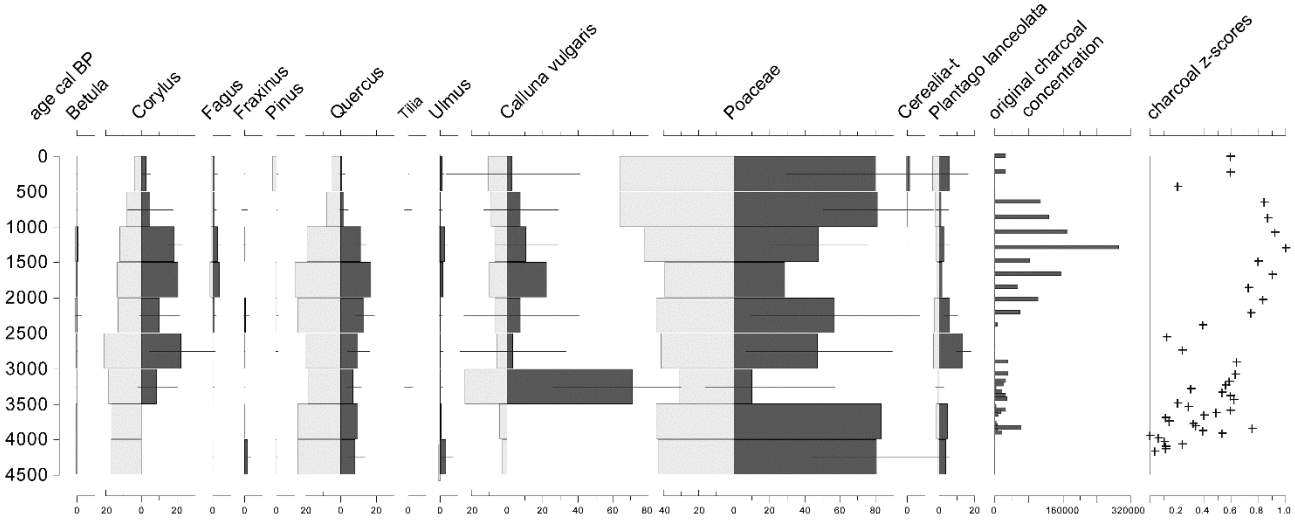


Figure S2-6: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from North Twitchen Springs, Exmoor (original data from Fyfe 2012).



Appendix S3. Spatial pattern of pollen percentages data from sites on Exmoor.

Figure S3-1: Maps of pollen percentage data for sites on Exmoor in 500-year time windows. This figure should be compared with LOVE estimates presented in Figure 3 (main article).